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The New World Species of Azolla¹

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The water-ferns, represented by Salvinia and Azolla, are among the most curious of plants, and would not ordinarily be taken to be related to the ferns. Salvinia plants consist of a shoot up to one or two inches long, with clusters of round floating leaves rarely as much as a centimeter in diameter. Azolla likewise is a floating plant, chiefly of the tropics; the entire surface of quiet ponds may be so covered by the tiny branching fronds as to exclude mosquitoes from the surface, and for this reason the plant is sometimes known as "mosquito-fern" (cf. Benedict, Amer. Fern Journ. 13: 48. 1923). These little floating plants send rootlets down into the water much in the manner of the duckweed (Lemna); their small size, branching habit, and the almost crystalline appearance of the tiny individual leaves may be judged from the accompanying drawings of living, non-fruiting plants from the greenhouses and out-door pools of the Brooklyn Botanic Garden (Pl. 6, fig. 1). The succulent leaves, in the center of which blue-green algae always live, gleam under the lens like leaves of Mesembrianthemum. In full sunlight the fronds often become reddish, but those in shaded localities remain bright green.

The branches of Azolla show a dorsiventral structure suggesting that of Selaginella. The leaves are two-lobed, the lower lobe being usually larger than the upper, mostly

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without chlorophyll and only one cell thick. These lower lobes are so adapted for floating the plant that water comes in contact only with their lower surface. The upper lobes do not reach the water at all. During the growing stage they are flattened in the same plane as the lower lobes, and it is only in age that they become somewhat erect.

As early as 1725, Feuillée had made crude illustrations of plants from the Peruvian region. Commerson, during his romantic voyage around the world with Bougainville (1767-1769), collected somewhere in the Magellan area the specimens upon which Lamarck in 1785 founded the genus Azolla, based on the single species A. filiculoides. No other species were known until 1810, when Willdenow described A. caroliniana, based on material derived from Richard in Paris, and therefore probably collected by Michaux in the southeastern United States. As yet, differentiation of species was based only on vegetative aspect, A. caroliniana being noted as having spreading leaves in distinction to the imbricate appressed leaves of A. filliculoides. In the same year that A. caroliniana was described, Robert Brown (Prodr. Fl. Nov. Holl. 167. 1810) placed the genus upon a scientific basis; both his genius and that of his artist, Ferdinand Bauer, contributed to the essential understanding of the reproductive bodies, as illustrated in Plate 10, accompanying the Botany of Captain Flinders' voyage (1814). Martius in 1834 beautifully illustrated A. microphylla Kaulf. (Icon. Pl. Crypt. Bras. pl. 74, 75), of which the figures are perhaps based on Brazilian plants, and Meyen followed shortly in 1836 (Beiträge zur Kenntniss der Azollen) with a fine series of drawings of A. filiculoides. It was not until 1847 that Mettenius², characterized by Christensen (in Verdoorn, Manual Pterid. 523. 1938) as the keenest fern student of the nineteenth century, published a

² In Linnaea 20: 259–282. pl. 2, 3. 1847.

monograph of the genus in which the species were carefully delimited. Unfortunately he did not describe and figure them from type material. Thus a change in the application of the names A. microphylla and A. mexicana may be necessary when the types can be studied, but I have found it expedient to follow his usage except in the interpretation of A. caroliniana. Since the time of Mettenius the systematic treatment of Azolla has gradually deteriorated; the elaborate work on the genus by Strasburger (1873) stressed details of cell structure and life history, but contributed nothing to taxonomy. The treatment by Baker (Journ. Bot. 24: 99–101. 1886) is decidedly inferior.

Most collections of Azolla will be found to be nonfruiting, but careful search under a low-power binocular microscope will frequently disclose megaspores not apparent in the first casual observation. The sori, when present, will be found in pairs in the leaf axils of older portions of the frond. Each sorus is completely surrounded by an indusium. In some species the inflated globose indusia of the microsporocarps exceed 1 mm. in diameter and can be seen with the naked eye; but the acorn-shaped indusium of the megasporocarp is much smaller and is completely filled by the rigid single megaspore and its appendages. Usually there will be a pair of microsporocarps, or of megasporocarps; occasionally the pair will consist of one of each, and this is the condition most frequently illustrated. Depending somewhat upon the species, the stalked microsporangia (borne within the indusium like a bunch of toy balloons) vary from seven or eight to nearly a hundred. Each microsporangium contains 32 or 64 imbedded microspores aggregated into four to ten spore-masses (massulae). The massulae are somewhat flattened (when four, they fit together in tetrads, like fern spores in general), and when

they are liberated from the microsporangium they display, in the New World species, the peculiar barb-tipped hairs (glochidia) which probably serve to anchor the floating massulae to the megaspores, and which are so necessary for the determination of the species. A compound microscope is necessary for examination of the glochidia. In the megasporocarp only a single megaspore develops. Wanda Pfeiffer has shown (Bot. Gaz. 44: 449. 1907) that initial microsporangia develop on the stalked base of the megasporangium, and that "if the megasporangium develops, there will be a megasporocarp; while if the microsporangia develop, there will be a microsporocarp." The lower bell-shaped portion of the megaspore is important from a taxonomic point of view, since it may be smooth, reticulate, or pitted. The upper portion or lid of the sporocarp comes off at maturity in a parachute-like manner, liberating the megaspore and disclosing the three-lobed "swimming apparatus" derived from non-functional megaspore material, formerly thought to give buoyancy to the megaspore. Development of gametes takes about a week. The microspores remain imbedded in the massulae during development; they produce antheridia, and from them antherozoids escape through the gelatinous substance of the massulae. The nucleus of the mature megaspore divides repeatedly to form a small embedded prothallus in which one or more archegonia are produced, each with an egg cell. The zygote develops after fertilization, and by continuous division produces the pinnately-branched floating sporophyte with which we started. Further details of the life-history are given by G. M. Smith (Crypt. Bot. **2**: 353–362. 1938).

This study was brought about by an attempt to identify material which I collected in abundantly fruiting stage in the Galapagos Islands in 1930. The specimens in the herbaria of the Brooklyn Botanic Garden and American

Fern Society were greatly augmented by the specimens in the United States National Herbarium, which Dr. Maxon kindly sent me, and selected specimens from the Gray Herbarium. The work was difficult, since it involved examination of glochidia and megaspores over the entire range of specimens, before the more abundant sterile material could be allocated to the individual species. Many collections of Azolla are so meager that identification is practically hopeless. When a series of fruiting plants has been recognized, the elongate-frondose character and curled leaves of well-developed A. filiculoides can be perceived at a glance. The dichotomous branches of A. caroliniana with their unusually small leaves are also characteristic; A. mexicana is of similar texture, but larger and more compact. A. microphylla, chiefly of tropical South America, occurs in general as small isolated somewhat elongate plants; these are frequently thickened and deep purple, though thin green plants are occasional, as in Drouet 2659 from Ceará, Brazil. The following treatment is of the American species only, all of which are characterized by the presence of glochidia on the massulae.

For identification of material the reader is especially directed to the photographs (Pl. 8) which illustrate typical specimens of the four species here discussed. The identity of the West Indian material must remain doubtful, for the specimens seen are all sterile; nevertheless, their relationship is with A. caroliniana, and they have been so identified by practically all previous writers. In A. filiculoides only the upper portion of an elongate frond is shown in figure 4; the leaves are most frequently of an ashy-gray color with broad, scarious, irregularly curled margins. In A. mexicana the under leaf lobes, which serve as floats for the plant, are frequently much enlarged, even more so than in A. caroliniana.

Nothing is known of the boundary between A. caroliniana and A. mexicana, which probably lies in the Texas-Louisiana region. Finally, the reader must not be too optimistic about the identification of sterile material. Usually, however, if the specimens are well collected and in a mature stage, they can be assigned to one of these four species. It is possible that microscopic studies of leaf margins may provide a key to the species, but thus far I have been unable to make any correlation.

SYNOPSIS OF SPECIES

A. Glochidia not septate; plants small (0.5-1 cm. diam.), dichotomously branched, the nearly orbicular, divaricate leaves small (0.5 mm. long), nearly smooth, not closely imbricate; microsporangia 8-40 in an indusium.—Eastern United States and the West Indies.

AA. Glochidia not septate, or rarely with 1 or 2 septae at apex; plants elongate (frequently 2-6 cm. long), with closely appressed, imbricate, papillose, oblong to ovate leaves (1 mm. long); microsporangia 35-100 in an indusium; massulae 4-6; megasporangia with raised, irregularly hexagonal markings.—Guatemala to Alaska; Andean and southern South America; occasionally introduced in the eastern United States, Hawaii, and Europe.

2. A. filiculoides (Pl. 6, figs. 1, 2; pl. 8, fig. 4).

AAA. Glochidia many-septate; plants dichotomously branched, 1-1.5 cm. diam., with upper leaf lobes 0.7 mm. long, the under ones much larger; microsporangia usually with 4 massulae; megaspore pitted.—Mexico and of scattered occurrence in the lowlands southward to French Guiana and Bolivia, northward to Utah and British Columbia, and eastward to Wisconsin and Illinois.

3. A. mexicana (Pl. 7, figs. 1-3, 5; pl. 8, fig. 2). AAAA. Glochidia many-septate; plants small (1-2 cm. long), pinnately branched, with nearly orbicular leaves 1 mm. long; megaspore smooth.—Chiefly in the lowlands of Brazil and British Guiana; of scattered distribution in western South America and northward to Central America, the West Indies, and "California."

4. A. microphylla (Pl. 6, fig. 4; pl. 8, fig. 3).

1. Azolla caroliniana Willd. Sp. Pl. 5: 541. 1810, not of later authors except as to some descriptions and illustrations of habit. ?A. portoricensis Spreng. Syst. Veg. 4: 9. 1827.

Ponds and slow streams, from Massachusetts and New York to Louisiana, and, judging from habit alone, Cuba, Puerto Rico, and Jamaica (Harris 10349). Jurgensen

229, from Santa Cruz, Rio Grande do Sul, Brazil, also has the habit of A. caroliniana.

Only in Tryon & Godfrey no. 907, from Clarendon County, South Carolina, and Garber's collection from Sanford, Florida, in 1876, did I find microsporocarps. The glochidia are non-septate, a condition otherwise characteristic of A. filiculoides, but somewhat smaller than in that species and acutely pointed at each end. Notwithstanding diligent search I have otherwise found no trace of fruiting bodies in this species. The sculpture of the megaspores, when they are seen, should be important for identification. Mettenius saw fruiting specimens of "A. caroliniana" only from Schiede's Mexican collection, which he illustrated.3 This I take to be A. mexicana cannot be considered as published. It was collected in January, 1820, "inter Serpillo et Estero," a locality close to the Tecoluta River, halfway between Vera Cruz and Tuxpan. In the synonymy of A. caroliniana, Mettenius cited A. mexicana Presl (Bot. Bem. Prague 150. 1844), which was based on Schiede's collection and represents the first actual publication of A. mexicana. Schiede's plant certainly has nothing to do with true A. caroliniana; nevertheless Mettenius' illustration was followed by Strasburger (1873) and later by Kuhn in Martius' Flora Brasiliensis (12: pl. 82. 1884), from which it was copied by Britton & Brown (Ill. Fl. 1: 35. fig. 76. 1896).

Schlecht. & Cham., which received no description and

⁴ Linnaea 5: 625. 1830. ⁵ Linnaea 4: 561. 1829.

⁶ This rarely accessible publication appears under the title "Obs. Botanicae" in Abh. Böhm. Ges. Wiss. V. 3: 150. 1845, and the description is as follows: "580. Nova Azollae species est: Azolla mexicana; fronde pinnata, foliolis imbricatis laevibus subrotundis coloratis, radicibus capillaribus. Habitat in Mexico, ubi legit clar. Schiede. Affinis videtur A. portoricensi, differt foliolis margine non hyalinis."

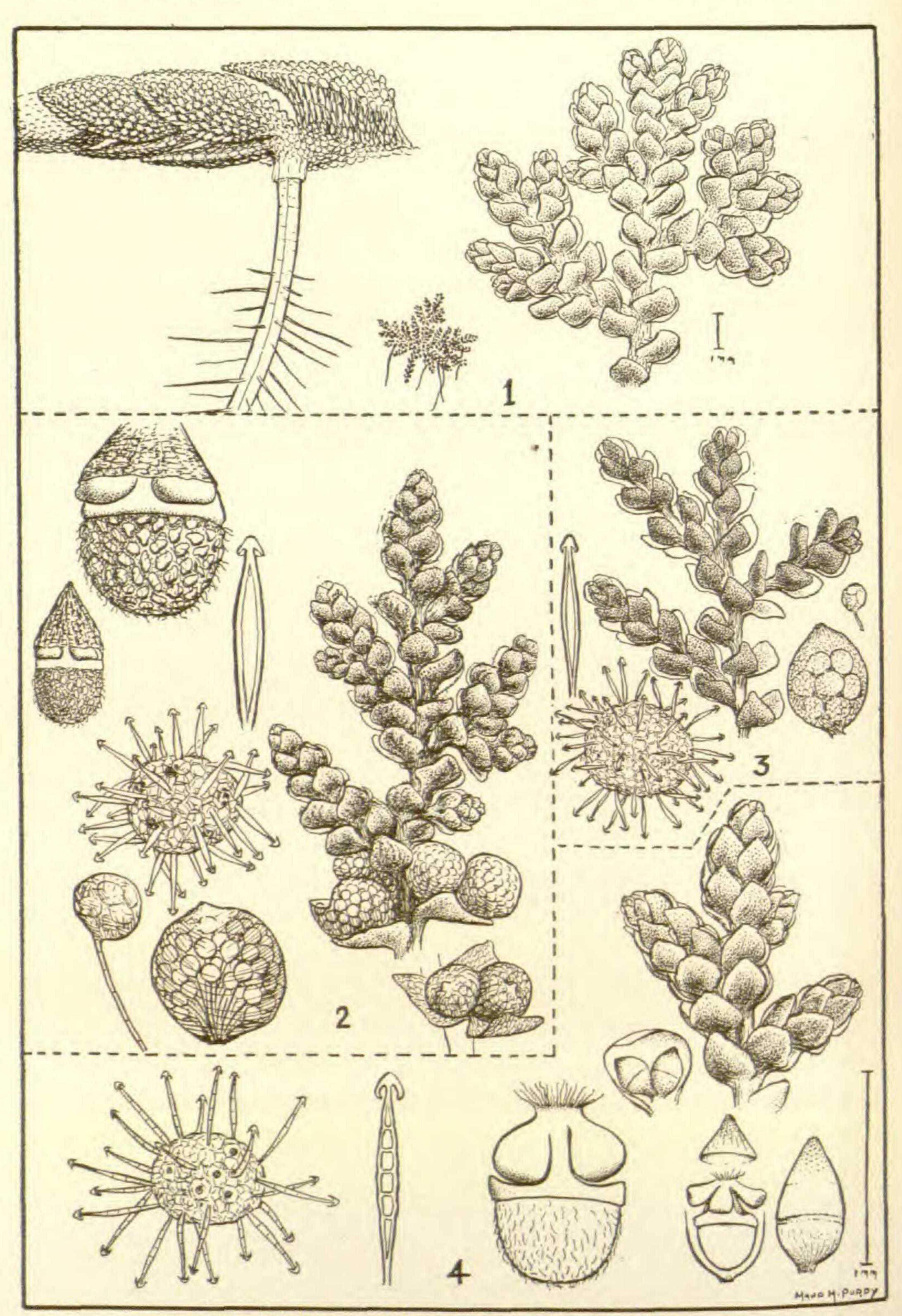


PLATE 6.—Fig. 1. Azolla filiculoides, from living material; fig. 2. A. filiculoides, California, Wheeler in 1941; fig. 3. A. caroliniana, South Carolina, Tryon & Godfrey 907; fig. 4. A. microphylla, Galapagos Islands, Svenson 86.

A. portoricensis was based on sterile material in the Sprengel herbarium, collected by Bertero.

2. Azolla filiculoides Lam. Encycl. 1: 343. 1783, and Ill. pl. 863. 1797; Meyen, Beiträge zur Kenntniss der Azollen, in Acad. Caes. Leop. Nov. Act. Nat. Cur. 18: 505–524. pl. 38. 1836; Strasburger, Ueber Azolla 78. pl. 6, figs. 87, 91. 1873; Kuhn in Mart. Fl. Bras. 1²: 658. pl. 82, figs. 9–11. 1884; Baker, Journ. Bot. 24: 100. 1886; Campbell, Ann. Bot. 7: pl. 8, figs. 27, 35, etc. 1893. A. magellanica Willd. Sp. Pl. 5: 541. 1810 (renaming of A. filiculoides); Mettenius, Linnaea 20: 277. pl. 3, figs. 16–21. 1847. A. squamosa Molina, Saggio Nat. Chile, ed. 2, 125. 1810, sec. Christensen. ?A. bonariensis Bertol. Misc. Bot. 21, in Rend. Sci. Bologna 1859–1860: 64. pl. 5, figs. 2a, 2b. 1860.

Azolla filiculoides came from the Magellan region, but the actual locality is uncertain. I have not been able to make out the distinctly annular markings of the megaspore shown by Mettenius; such markings are usually angular and are better shown by Strasburger (pl. 6, figs. 91, 92). Azolla bonariensis was described from Buenos Aires, based on a collection by Fox-Strangwais, and is referred to A. caroliniana by Christensen (Ind. Fil. 148. 1906). Schlechtendal (Bot. Zeit 19: 343. 1861) does not seem to value it highly, nor can Bertoloni's work as a whole be held in very high esteem.

Occasionally specimens are found in which there are one or two septae at the very apex of the glochidia, but these may be residual protoplasmic material rather than actual septae. This form is A. filiculoides var. rubra (R. Br.) Strasburger (Ueber Azolla 78. pl. 6, fig. 86a. 1873), based on A. rubra R. Br. (Prodr. Fl. Nov. Holl. 167. 1810; Baker, Journ. Bot. 24: 100. 1886). It was originally described from Australia, but is of little if any importance geographically, since it is found scattered throughout the range of the species in America.

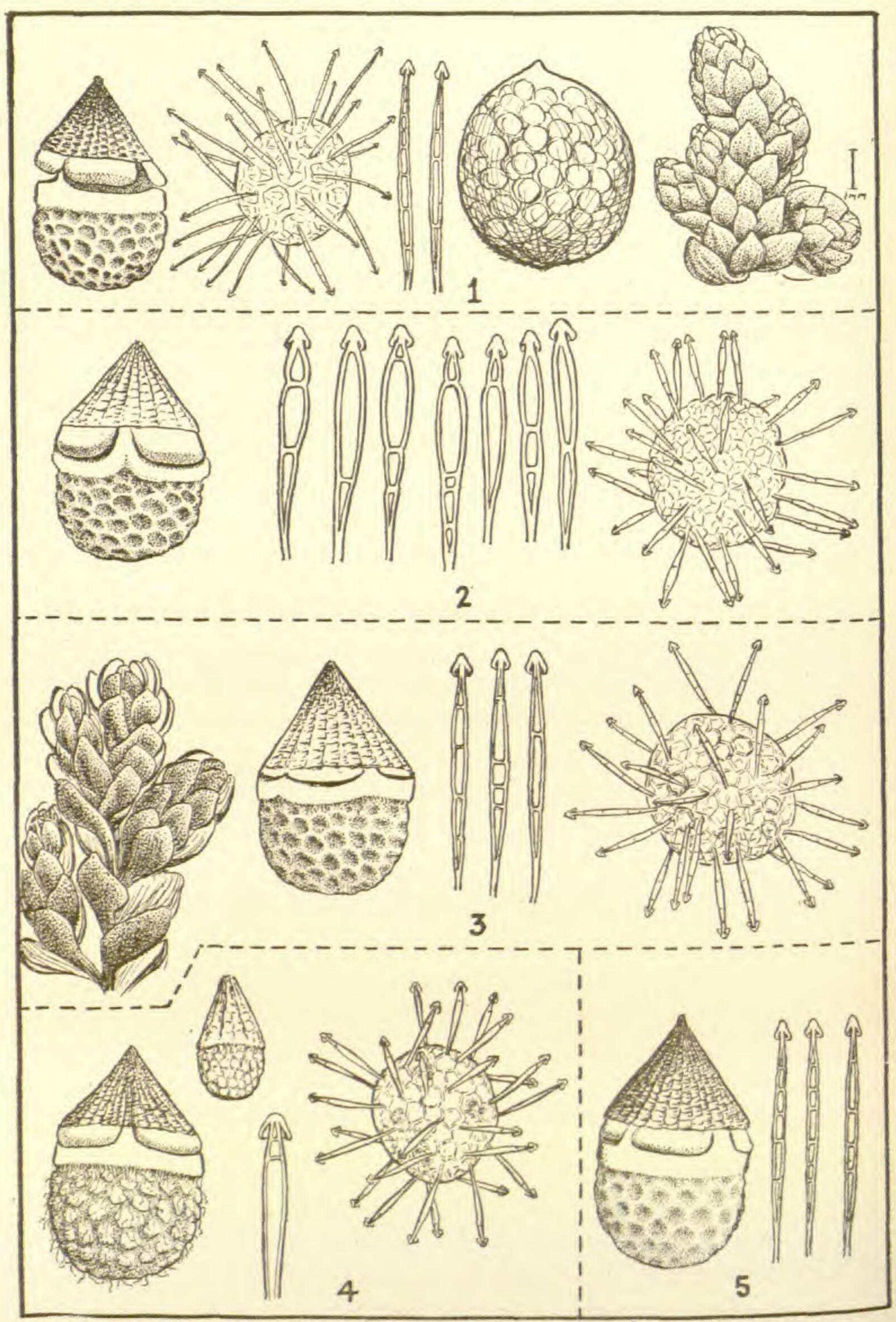


Plate 7.—Fig. 1. Azolla mexicana, Bolivia, Cárdenas 2760; fig. 2. A. mexicana, Washington, Suksdorf 1216; fig. 3. A. mexicana, Oregon, Nelson 4176; fig. 4. A. filiculoides var. rubra, Chile, Looser in 1930; fig. 5. A. mexicana, Mexico, Rose 14647.

Azolla filiculoides seems to be the only species known from Argentina, Uruguay, Chile, and from the Andes. In the Andes it seems frequently to grow on a rather dry substratum, the plants being often aggregated in thick masses, with very prominent roots. Such specimens are: Bogotá, Colombia, Apollinaire in 1907; Chasquí, Peru, Macbride 3307; Quispicanchi, Peru, Herrera 2616, 2618; Bolivia, R. S. Williams 2648; Valparaiso, Chile, Claude Joseph 1562, 4698; Concón, Prov. Aconagua, Chile, Looser in 1930.

I have seen the following collections of A. filiculoides in fruit: Alaska: Bischoff in 1868. New York: Brooklyn Botanic Garden, Benedict in 1924. Riverhead, Long Island, Muenscher & Curtis 6647. California: Pacheco Pass, Brewer 1288. San Francisco, Rose 42246; Bolander in 1865 and 1866. San Mateo County, Blake 9944. Merced County, Howell 4206. Santa Cruz County, Abrams 1833. San Luis Obispo, Summers in 1889. Santa Barbara, Gambel 668. Los Angeles, Wheeler in 1941. La Grange, Tracy. San Bernardino, Parish 5278. San Jacinto, Leiberg 3104. San Diego, Kimball. Mission Dam, San Diego County, Kimball 229. Hot Springs, San Diego County, Vasey 694. ARIZONA: Tueson, Thornber in 1903. Mexico: Chihuahua, Hartman 614. Puebla, Arsène in 1907. Morelos, Rose & Painter 6878. Guatemala: Dept. Sololá, Muenscher 12179. Colombia: Bogotá, Lehmann 6363. Bolivia: Cochabamba, Julio 191; Bang 983, 1032, 1033. CHILE: Santiago, Hastings 319. Valdivia, Philippi in 1888. Brazil: Rio Grande do Sul, Malme 290. Uruguay: Florida, Rosengurtt B-781. Montevideo, Gibert 1317, 1318. ARGENTINA: Jujuy, Eyerdam & Beetle 22193, 22335. Corrientes, Palmer 1854. Rioja, Venturi 8230. Río Negro Valley, Fischer 233. HAWAII: Oahu, Degener & Dowson 12913. Honolulu, Fosberg 13833.

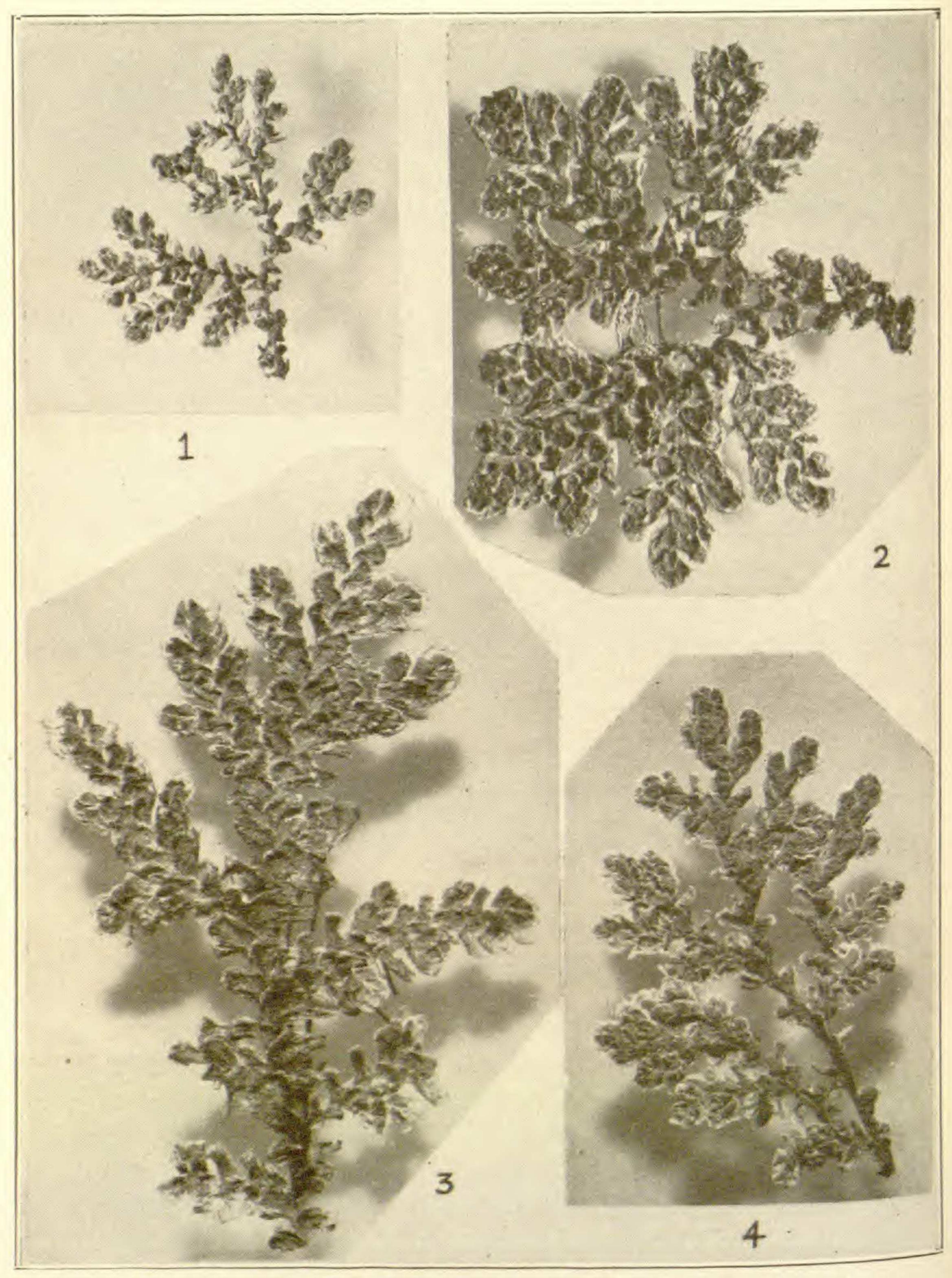


PLATE 8.—Fig. 1. Azolla caroliniana, South Carolina, Tryon & Godfrey 907; fig. 2. A. mexicana, Mexico, Rose 14806; fig. 3. A. microphylla, Galapagos Islands, Svenson 86; fig. 4. A. filiculoides, Argentina, Venturi 8230. All about 5 times natural size.

3. Azolla mexicana Presl, Abh. Böhm. Ges. Wiss. V. 3: 150. 1845. A. caroliniana sensu Mettenius, Linnaea 20: 278. pl. 3, figs. 9-15. 1847; Kuhn, in Mart. Fl. Bras. 1²: 659. pl. 82. 1884; Britt. & Brown, Ill. Fl. 1: 35. fig. 76. 1896, not Willd. A. mexicana Schlecht. & Cham. Linnaca 5: 625. 1830 (name only). ?A. densa Desv. Mém. Soc. Linn. Paris 6: 177. 1827 (cited in synonymy by Mettenius).

Azolla mexicana resembles A. caroliniana in its flattened, dichotomously branched appearance, and it includes in general the specimens from the western United States and Mexico cited by authors under the name A. caroliniana. The leaves are, however, larger than those of A. caroliniana and do not have their slender appearance. The megaspores, before they are mature, might sometimes be mistaken for those of A. filiculoides because of the greenish corky-thickened markings, but when the megaspore has become dull gray and relieved of its outer covering the surface will be seen to be minutely pitted. This is undoubtedly the impression Mettenius wished to convey in his illustration of A. caroliniana, which, as I have mentioned previously, was drawn from a Mexican collection.

According to Weatherby (Contr. Gray Herb. 114: 21. 1936), no specimens of Azolla densa Desv. or A. arbuscula Desv. are to be found in the Desvaux Herbarium. The only two sheets of Azolla are named A. caroliniana and A. filiculoides, and these identifications are confirmed by Kuhn. It seems that the names A. densa and A. arbuscula can well be disregarded.

I have seen the following collections in fruit: Wisconsin: Lacrosse, Hale in 1861. Illinois: Carroll County, Waite in 1887. Oquawka, Patterson. Swan Lake, Calhoun County, Metcalf 1110. Missouri: Cooley Lake, Clay County, Metcalf 1045. Utah: Provo, Garrett in

1926. Nevada: Carson Sinks, Sperry & Martin 782. British Columbia: Sicamous, Macoun 14205. Wash-INGTON: Klickitat County, Suksdorf 1216. Oregon: Clackamas County, Nelson 2761. Salem, Nelson 4176; Peck in 1920; E. Hall 698. CALIFORNIA: Pitt River, Modoc County, Gilbert. Alturas, Modoc County, Wheeler 4013. Palo Alto, Ward in 1899. Santa Clara, Wilkes Exped. San Diego, Cook in 1921. Mexico: Guadelupe, Sinaloa, Rose 14806. Rosario, Sinaloa, Rose 14647. Morelia, Michoacán, Arsène 1208, 2363; Rosenstock Exs. 73. Honduras: Tela, Blake 7281. Costa RICA: Cartago, Anderson 17532. FRENCH GUIANA: Leprieur in 1838. Bolivia: Charagua, Oriente, Cárdenas 2760. Without mention of any state or collector, there is a specimen in the Gray Herbarium from "2 miles south of Columbus, overflow of Canal by Morrells, Sept. 18, 1841."

4. Azolla microphylla Kaulfuss, Enum. Fil. 273. 1824; Martius, Icon. Pl. Crypt. Bras. 123. pl. 74, 75. 1834⁷; Mettenius, Linnaea 20: 276. pl. 3, figs. 1–8. 1847. Salvinia Azolla Raddi, Pl. Bras. 1: pl. 1, fig. 3. 1825.

Azolla microphylla was supposedly collected by Chamisso in California, but in the numerous collections which I have examined from that state I have seen no trace of it in the traditional sense of Mettenius. But there is difficulty, since Mettenius derived his idea of the glochidia of A. microphylla from Martius, whose illus-

⁷ The megaspore as illustrated by Martius is not smooth but reticulate, as is sometimes seen in young megaspores of A. mexicana. It was possibly drawn from the original material collected by Chamisso. Martius states (p. 125) that no wholly mature material of the calyptra had fallen under his observation. On page 126, he notes that A. microphylla occurs throughout much of Brazil, especially in the tropical parts; that Poeppig has sent him specimens from Las Piedras in Cuba and others have sent him material "in aquis camporum (Savanes) australiorem invenientam"; and that Roemer has sent him material collected by Chamisso in California. See the discussion under A. mexicana above.

trations were supposedly based on Brazilian material. In addition, the megaspores which Mettenius illustrated came from Cuba, a region from which I have seen only the sterile specimens referred to A. caroliniana. If the Chamisso specimen, which was fruiting, is ever examined, I suspect it will turn out to be either A. mexicana or A. filiculoides; Mettenius' drawing of the smooth megaspore, on the other hand, may possibly represent the unknown megaspore of A. caroliniana. The description by Kaulfuss was brief: "A. frondibus orbiculatis semipinnatis pinnis trilobis, foliolis imbricatis adpressis minutis. Frondes tri-quadrilineares orbiculatae subradiatae, folia papillosa arcte adpressa minutissima hyalina. Capsulae globuliferae semine papaveris fere duplo maiores."

Azolla microphylla was separated with difficulty by Mettenius from A. cristata Kaulfuss (Enum. Fil. 274. 1824), which was based on sterile material from Kunze's herbarium (without collector's name) from Demerara, British Guiana. Evidently Mettenius was able to find fruiting material, for he differentiated A. cristata by the crested-ciliate lid of the megaspore, well illustrated in his account (Linnaea 20: 278. pl. 2. 1847). The number of massulae in a microsporangium, which Mettenius gives as 6 in A. microphylla and as 4 in A. cristata, would seem of little value for diagnosis of species, since the number is variable, being 9 or 10 in my Galapagos collection.

Chamisso, who made the original collection of A. microphylla, was even better known as a writer than as a botanist, and is especially remembered for the story of Peter
Schlemiel, the man who sold his shadow. He was a
member of the French aristocracy driven out during the
Revolution, who migrated to Germany and to Switzerland. In 1815 he embarked from Copenhagen aboard
the Rurik on a 'round-the-world expedition under the
patronage of Count Romanzoff and under the command

of Lieutenant Kotzebue of the Russian Navy. They explored the vicinity of St. Catherine on the Brazilian Coast, where heavy rains made collecting almost impossible, but where they obtained a goodly number of new ferns; the coast of Chile, where they arrived to find the vegetation burned up by summer heat; the California coast where, according to Jepson (Madroño 1: 253. 1929), they explored the San Francisco peninsula during October, 1815. From the last locality, therefore, Azolla microphylla is supposed to have come. Then they sailed for the Hawaiian Islands and to the Aleutians, where in futile searching for a Northwest Passage they had their greatest success in botanical collecting. Kaulfuss wrote up the "Enumeratio Filicum" from this voyage; Chamisso's life, especially as to his botanical activities, is reviewed by Schlechtendal (Linnaea 13: 83-112. 1839). An additional account of Chamisso has recently been published (Calif. Acad. Sci., Occasional Papers No. 20, 1943).

The following collections of A. microphylla have been seen, most of them in fruiting condition: Dominican Republic: Haina River, Faris 413.8 El Salvador: Santa Emilia, Dept. Sonsonate, Standley 22121. British Guiana: Botanic Garden, Georgetown, Bailey in 1921; Hitchcock 16540. French Guiana: Swamps of Río Appruague, Leprieur in 1834. Galapagos Islands: Charles Island, Stewart 3441. Indefatigable Island, Svenson 86. Peru: Loreto, Killip & Smith 27707. Bolivia: Gran Chaco, Tatarenda, Fries 1397. Brazil: Maranguape, Ceará, Drouet 2659. Minas Geraes, Regnell III. 1507. Rio Grongogy Basin, Bahia, Curran 206. Toca de Onca, Bahia, Rose 20128.

⁸ This is perhaps a casual introduction; it does not represent the ordinary West Indian plant with habit of A. caroliniana.